ORGANIC EVOLUTION AND THE SIGNIFICANCE OF SOME NEW EVIDENCE BEARING ON THE PROBLEM

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I

THE biological problem recognized as having the greatest fundamental importance at the present period is that problem of evolution relating to the means by which the heritable characters differentiating various organisms from one another were first called into existence, or granting the validity of the gene hypothesis and speaking more concisely, how hereditary character-forming genes have originated in the process of evolution. That the diverse forms of life found upon the earth are only to be explained as the result of organic evolution, is a proposition which scarcely needs be mentioned at the present period in the history of science, at least so far as individuals endowed with minds reasonably logical in evaluating evidence are concerned. It is not evolution as a process going on in the world which is being particularly questioned nor the general method by which characters once having originated are inherited, but the particular method by which heritable characters first arose.

The purpose of the essay here presented is threefold. *First,* that of pointing out the unsatisfactory nature of much of the earlier evidence as a basis for sound generalizations in connection with a clear understanding of evolution. *Second,* that of calling attention to the serious shortcomings of modern methodology in throwing light on the causative factors of evolution. *Third,* that of presenting some new evidence somewhat unique in its nature, based in part on preliminary experimental work, to

the effect that the environment acting through long intervals of time may impress characters upon an organism which become unalterable by reversal processes.

To these propositions may be added the suggestion of the fundamental importance which physico-chemical methods must play during the future in solving the problems of evolution.

II

The controversies relating to evolution have been many. When, however, one considers the interest attached to the subject, its broad bearing on various phases of human welfare—sociology and economics in general, animal and plant breeding in particular—together with the difficulties of interpretation which apparently have increased rather than diminished during the sixty or more years seriously devoted to its elucidation, it is not at all surprising that many different conclusions have been reached, many dogmatic statements presented, and many acrimonious discussions engendered.

In connection with a clearer understanding of the points at issue, it will be well to pass certain historical details relating to the development of the different theories somewhat critically in review. This is done even at the risk of a repetition of facts quite familiar to those who have taken more than a passing interest in the subject.

For long the theory of natural selection dependent on the inheritance of small chance variations received general acceptance. Championed by Weismann in his notable controversy with Spencer to the exclusion of the Lamarckian idea that characters acquired through environmental stimuli were heritable, it seemed at the time entirely plausible as an explanation meeting the conditions.

With the greater attention given to experimental methods, however, doubt arose concerning the fundamental value of selection and resulted in the presentation of the mutation theory by DeVries. Here evolution was inter-

preted as arising from sudden and comparatively extreme variations passed on by inheritance in nearly an unchanged condition. Once more the results of experimental work along the lines of the rediscovered principle of Mendelian segregation indicated to a large number of students of evolution that the facts set forth by DeVries were subject to quite another explanation, in itself having no bearing on the origin, but merely on the redistribution of the character-forming units already present in the stock utilized. Another explanation not taking into account the purity or impurity of the parental stock, accounted for "mutations" through the sudden ineffectiveness or loss of a gene.

The dissatisfaction thus arising resulted in the return of many to the fold of "acquired characters." Semon (1912) reviving the "mneme" principle received the support of Wettstein, Przibram, and others. A disinclination existed, however, among most naturalists to accept the evidence presented as seriously upholding the inheritance of new characters produced by environmental stimuli. Explanations of the results on quite other grounds seemed more plausible. For example, the work of Tower (1906), (1910), etc., in attempting to control the color pattern of the potato beetle by changes in temperature and humidity, encountered the impurity of the germplasm objection as well as the gene loss objection, either one of which would be fatal to the validity of the conclusions, if sustained. Commenced at a period in 1895, prior to the rediscovery of the principles dealing with alternative inheritance, and finished in 1904 before the facts were duly appreciated, it is not at all improbable that genetic complications in the way of recessives, modifiers, losses, lethals, etc., were involved. The destructive criticism presented by Cockerell, Gortner, Bateson, Castle, and others, particularly in reference to the later studies of Tower (1910), makes it evident that the results must be confirmed from independent sources with more consideration to the possible errors mentioned before the conclusions are to be accepted.

Similarly, the work of MacDougal (1907), in connection with the modification of *Raimannia odorata,* one of the Patagonian primroses, may be explained. Compton, as noted by Bateson (1912), using the same species, was unable to obtain like results, while Humbert (1911) utilizing 7,500 pure line plants of *Silene noctiflora,* one of the "pinks" also failed to obtain so-called "mutants" similar to those found by MacDougal.

The investigations of Kammerer, Woltereck, Ferroniere, etc., are of decided interest, but to those critically inclined they offer no evidence giving pronounced support to the proposition that environmental stimuli form new genetic factors.

Thus, in turn, have the theories as to the method by which evolutionary progress occurs been undermined by doubt. Feeling the insufficiency of small chance variations, of environmental variations, and of larger germinal variations, as a summation process, it is not to be wondered that the truth-seeking pilgrim has become wearied in his journey and longs for a more secure resting place.

III

Let us return to the problem as suggested in the opening paragraph, namely the actual origin of heritable characters, and consider somewhat more carefully as to whether theories exist justified by facts, which will furnish acceptable evidence. There are two well-developed hypotheses, the general one of DeVries and the more specific one of Morgan and his associates, founded on discontinuous variations, and that of Castle based on continuous variations.

Considering the views of DeVries and his followers in the light of experimental investigations made during the last ten years, it has become more and more evident that by far the greater number, if not all, of the so-called mutations thus obtained, were explainable on the basis of the combinations of preexisting units of the germ cells. This rests upon the proposition that there are present in the

gametes certain hypothetical entities to which the name gene or factor has been applied and which give rise to the heritable characters of an organism. Thus it is at once recognized that the problem relates to the origin of the gene, rather than to the origin of the apparent characters with which it is correlated, and that by far the greater number of so-called new characters are not new, but were performed at remote periods of time. So far as the present arguments are concerned, it matters not whether the results are assumed to be brought about by material units or enzyme reactions. The prepared potentialities exist in either case.

As examples of extreme types of characters which may arise from the combinations of existing genes and which might have been considered "mutations" at an earlier period when the facts as to their origin were not fully known, one need only mention the "blue" of the Andalusian Fowl exhibited by the hybrid between the black and white parental stock, or the "pink" presented by the cross between the red and white "four-o-clocks" of Correns. A type of characters more in line with mutations which have been described and to which there is every reason for believing that many of them may be referred, rests upon multiple gene effects combined with sterility, in accordance with evidence presented by Davis, and others. Of decided interest in this connection is a recent paper by Muller (1917) calling attention to "An *Œnothera*-like case in *Drosophila*" where a result quite comparable to certain mutations of *Œnothera* is explained through the action of balanced lethal genes. There are other varying degrees of combinations from which "mutant" characters may arise and which depend on the behavior of the genetic material in connection with recessives, modifiers, lethals, crossovers, non-disjunction, etc.

There is really nothing extraordinary in the appearance and disappearance of the characters thus formed, beyond their interpretation, and this has furnished false premises for many erroneous conclusions, chief of which,

in the opinion of the writer, is the mutation theory as outlined by DeVries in so far as it may account for progressive evolution.

Inasmuch as it seems probable that the results obtained by Castle are to be explained upon the same basis as those of DeVries, it will be well to consider them in this connection. Here it is assumed that a continuously variable heritable gene is involved, and that progressive results are obtained through the selection of the "unit characters" produced by such a gene. Castle, however, stands almost alone in vigorous support of such a variation, while opposed to him are the Hagedoorns, Morgan, Pearl, Punnett, McDowell, Muller and others equally insistent that genes once having originated pass on from one generation to another unchanged except in comparatively rare instances where so-called "mutations" occur.[1] It is maintained by those advocating this view that the results in connection with hooded rats on which Castle bases his contentions, are due to an uncertain number of modifying genes not in themselves variable, and that the existence of such genes has been demonstrated in other organisms presenting results similar to those obtained in rats. The work of Little (1917) with mice where three segregating types of spotting were found to produce varying degrees of color pattern, indicates that multiple genes are involved. Furthermore, the analysis by Little of the data obtained by Castle, Phillips and Wright, points decidedly to the interpretation of their

[1] Jennings (1917) has recently endeavored to show that the views of Castle and his opponents are identical. This, however, is by no means the case. On the one hand there is the idea of a continually variable gene (coat-color-producing gene in rats) moved gradually along a given scale by selection. On the other hand there is the idea of a rarely mutating gene (*e. g.*, sex-limited eye color producing gene in *Drosophila*) moving abruptly from one part to another of the scale. Its position once obtained remains for a long time constant. These differences of interpretation are at present irreconcilable.

Since this note was written, Morgan (1917) has discussed the matter in detail, presenting arguments quite similar to those mentioned above, and arriving at a similar conclusion.

results on the basis of multiple genes instead of a continually varying gene.

It would thus appear evident that the theory outlined by Castle is open to quite the same objections that occur in connection with the mutation theory of DeVries, and that there is little evidence for believing that it has any fundamental value in explaining evolution.

The mutation theory of Morgan and his associates, based primarily on results obtained in studies of the small "fruit-fly" *Drosophila,* apparently presents quite another view of the subject. Here it is clearly indicated that evolution has taken place through the incorporation of mutant changes, and that these changes are due to discontinuous "mutations" of genes as exemplified in multiple allelomorphs.

Assuming the validity of the arguments based on linkage relations in respect to the localization of the genes, the conclusion follows that the "mutation" results either (1) from a change in a specific gene or (2) from the complete linkage of a series of genes. If the latter proposition should be the correct interpretation, and it is by no means clear that it is not, the objections urged against the theories of DeVries and of Castle hold equally here.

Morgan and several others have presented evidence for believing in the specific change of a gene. Granting that this is the actual explanation of the facts presented in connection with multiple allelomorphs, etc., there are two lines of argument leading to the conclusion that these changes are results of combinational sub-units or sub-genes existing in the species, and that progressive evolutionary changes are no more represented here than in the previous theories of DeVries and of Castle.

The first argument (*a*) rests upon the recurrent "mutations" which have been noted in a considerable number of cases. Thus the sex-linked eye colors of *Drosophila* forming the multiple allelomorph system consisting of white, eosin, cherry, blood, tinged, and buff, and their dominant allelomorph, red, of the wild fly, have their

origin from a single definite area or locus in the "X" chromosome, accepting linkage as a criterion. They have not arisen in a continuous series but as sudden changes from one extreme to another at comparatively long intervals. The character may remain modified in one direction and then suddenly revert to an original condition. Thus white changed to eosin and later back to white as noted by Morgan (1916). Furthermore, the changes are not extremely infrequent. A similar transformation has been noted by Emerson (1917) in maize where self color apparently changed to variegation and later back to self color. A variation which may be of the same type has been described by Shull (1911) for *Lychnis*. Quite recently Zeleny (1917) in studies on *Drosophila melanogaster* Meig. (=*ampelophila* Löw)[2] has noted a reversed mutation where full-eyed flies result from the return of the bar gene to the original full-eyed condition. In each of the cases mentioned the germinal purity of the stock was believed to be without question.

Such results are not to be attributed to a continuous series of mutations, to progressive changes, or to genetic losses. They clearly suggest that the gene, if it is the individual gene which is involved, is made up of smaller combinational units which through their permutations give rise to the characters in question. Presumptive evidence is certainly furnished against the idea that anything new has developed in the organism to form the particular characters. Furthermore, one may well believe that any particular mutation under observation sufficiently long, will exhibit recurrent changes.

The second argument (*b*), to the effect that the gene is comparatively stable and that "mutations" are only transitory combinational changes, is based on the maintenance of apparently identical genes through long periods of time. Thus Metz (1917) found that the three mutations which had, up to that time, occurred in *Drosophila virilis* Sturt. appeared exact duplications of the

[2] Sturtevant, mss.

mutations in *Drosophila melanogaster* Meig.[3] In both species "confluent," a modification of the wing venation, is similar in form, dominant over "normal" and "lethal," when the fly is homozygous for the character. The characters "yellow" and "forked" are sex linked in both species and otherwise alike so far as the evidence exists. Inasmuch as the earliest representative of *Drosophila* thus far known is a species not decidedly different from those now existing as noted by Löw (1850), who described it from the amber of the Baltic Sea, and belongs to the Lower Oligocene of the Tertiary Period, with an age of from two millions to three millions of years, one must infer that the genes common to the two species mentioned have been preformed for a long period of time, and that nature has paid little attention to such mutational changes as occur in connection with multiple allelomorphs.

There are certain investigations widely separated as to their content, but apparently closely correlated as to the underlying explanatory principles involved, which must not be overlooked in a consideration of the changes which may take place in hereditary units. These are concerned with the differences involved in metabolism.[4]

On the one hand there are studies dealing with the direct effects of a changed metabolism on the developing individual. Here may be mentioned the work of Lillie in connection with the "free-martin" of cattle; Steinach on the transplantation of the gonads in rats and guinea-pigs; Goodale on the grafting of ovaries in male fowls; Pearl and Surface on the degeneration of the ovary in cattle; Riddle with pigeons, etc. On the other hand, there are studies dealing with the indirect effects on inheri-

3 The species are distinctly separated not only in external appearance but also by their chromosome number. *D. melanogaster* has four pairs, while *D. virilis* has five pairs of chromosomes.

4 The theory has had a long historical development. Treat (1873) published a paper on controlling sex in butterflies as a result of food supply. Yung (1881) worked with tadpoles. Nussbaum (1897) with rotifers. Recent evidence of an elaborate nature has been presented by Goldschmidt, Woltereck, Whitney, Banta, Shull and others.

tance. Among these may be mentioned that of Goldschmidt with moths; Woltereck with daphnids; Plough with temperature effects on *Drosophila*; Hoge with the effects of cold on *Drosophila*; Morgan with the effects of moist food supply on *Drosophila*, etc.

As an example of the development group, the investigation of Lillie may be noted. The evidence obtained showed that the "free-martin" or sterile female usually developing where the twins are of separate sexes in cattle, etc., resulted from the modifying influences of the sex hormones in the male where the two chorions had anastomosed.

As an example of the inheritance group, Morgan has found that the "mutant" "abnormal abdomen" in *Drosophila* occurs in connection with a moist food supply. The character is a sex-linked dominant. If an abnormal male is bred to a normal female and the food is kept moist, the sons are normal and the daughters abnormal. If the food is dry both sons and daughters are normal. The reciprocal cross gives sons and daughters both abnormal with moist food but normal with dry food.

It follows then that in *Drosophila* the gene for the abnormality—or the chemical preparedness for the inhibition of normality, if one so wishes to term it—is performed in the "X" chromosome and merely awaits a suitable environment before presenting itself as a character. Similarly, in connection with the changes occurring in the development of the "free-martin" of cattle, it seems necessary to admit that there are genes present in the sex chromosome concerned with the development of sexual characters which, however, are in a state of equilibrium, and that the inhibition or the excitation[5] of one or the other genes or groups of genes will result in the development of the corresponding individual.

From the facts presented, one seems justified in making the deduction that heredity hands down a framework

[5] It has been shown by Chapin (1917) that the gonads of the free-martin originally destined to be a female, attain a male condition.

which within certain limits allows a plasticity in the development, and that the direction of development is determined by physico-chemical influences through the suppression of potential units.

Thus the conclusion seems almost unavoidable that by far the larger number, if not all, of the heritable characters making up an organism, result from combinational units which have long been predetermined, and that the breeder, whether the semi-scientific agriculturist or the ultra-scientific drosophilist, is largely, if not entirely, engaged in presenting new combinations of existing units. If this be true, modern genetics has left the actual problem of evolution far to one side and deals only with results of a secondary, although none the less interesting, nature.

One is, therefore, led to inquire as to whether there may be available evidence which will permit a new insight into conditions governing the formation of characters, even though the evidence from its nature must be largely circumstantial.

IV

Accompanying the progressive swimming movement of most aquatic microorganisms there is a characteristic axial rotation. This has been noted by Nägeli, Engelmann, Strassburger, Mast and more in detail by Jennings (1901) who has called attention to the value which such a compensatory motion may have for the organism in which it exists. No explanation has been suggested other than this as to the origin of the rotation, and without further thought it is evident that one would be inclined to attribute it to natural selection, assuming that those individuals in which it did not occur were at a disadvantage in the struggle for existence by reason of their more confined movement.

It is the phase of the question dealing with the particular causes bringing about the rotation that appears to be of extreme significance when considered in connection with the principles underlying evolution and to be

susceptible to quite another explanation than the natural selection implied by the term "adaptiveness" which, in accordance with Jennings (1906), is based on the idea that "it tends to preserve the life of the animal." Furthermore, when the groups of facts associated with the characteristic rotation are brought in review, it would seem that the explanation suggested may go far toward interpreting the origin of the fundamental activities as well as the origin of the characters in general of organisms.

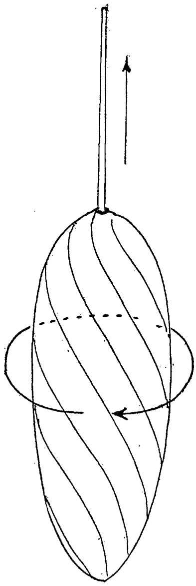


FIG. 1. Typical Euglenoid Flagellate illustrating left-hand spiral arrangement of striæ in connection with clockwise rotation (observer in front) and progressive movement by means of anterior flagellum.

In connection with the preparation of a systematic review of the order Euglenoidina belonging to the class Flagellata of the Protozoa (1915), it was noted with decided interest that a large number of the forms possessed an oblique striation ranging from almost indiscernible markings to characters of great complexity impressed upon a cellulose-like envelope (*e. g.*, *Euglena spirogyra* Ehrenb., *Phacus pyrum* (Ehrenb.), *Heteronema spirale* Klebs, etc.), the striæ extending forward and to the left. The character also appeared to be invariably correlated with an axial rotation of the organism from right over to left (Fig. 1). Such a movement is to be described in physical terms as "clockwise," the position of the observer being in front of the advancing organism.

The facts took on additional interest when it was noted that forms with a reverse striation seemed entirely absent from the northern hemisphere, although such forms existed in the southern hemisphere.

Inasmuch as the euglenoids are in general positively phototactic under normal conditions, it would immediately occur to one seriously considering the question, that

the underlying principle producing the rotation was the turning of the earth on its axis, with the resultant apparent motion of the sun from east to west. Such a hypothesis would become the more tenable when it was found that negatively phototactic microorganisms of the northern hemisphere rotated as a rule in a reverse or counter-clockwise direction.

Some of the evidence thus far obtained may be presented more clearly in tabular form[6] (Table I). Thus

TABLE I

A series of aquatic microorganisms showing in general the clockwise rotation of positively phototactic forms and the counter-clockwise rotation of negatively phototactic forms in the northern hemisphere, with evidence for the tendency to reverse condition in the southern hemisphere.

Northern Hemisphere		
Euglena viridis Ehr.	Positive.	Clockwise.
Euglena hæmogranulata Walt.	Positive.	Clockwise.
Euglena tripteris Duj.	Positive.	Clockwise.
Euglena spirogyra Ehr.	Positive.	Clockwise.
Leptocinclis ovum (Ehr.)	Positive.	Clockwise.
Phacus pyrum (Ehr.)	Positive.	Clockwise.
Cryptomonas ovata Ehr.	Positive.	Clockwise.
Pandorina morum (Müll.)	Positive.	Clockwise.
Eudorina elegans (Ehr.)	Positive.	Clockwise.
Volvox globator (Linn.)	Positive.	Clockwise.
Stentor polymorphus Ehr. (= *viridis*)	Positive.	Counterclockwise.
Phacus longicauda Ehr.	Positive.	Counterclockwise.
Stentor cœrulus Ehr.	Negative.	Counterclockwise.
Anurea cochlearis Gosse	Negative.	Counterclockwise.
Arenicola cristata (larva)	Negative.	Counterclockwise.
Chilomonas paramœcium Ehr.[1]	Negative.	Counterclockwise.
Southern Hemisphere		
Leptocinclis piriformis Cun.	Positive?	Counterclockwise.
Phacus bacillifer Cun.	Positive?	Counterclockwise.
Leptocinclis mammilata Cun.	Positive?	Clockwise.

it may be stated that so far as the facts are available, positively phototactic forms with the exception of

[6] The rotation direction and light responses noted are those taking place under normal conditions. The conclusions presented are not altered by the fact that as a result of stimuli under conditions imperfectly known, reverse movements may occur, *e. g.*, the negative response of Euglenoids to intense light.

Stentor polymorphus Ehrenb. (=*S. viridis* aut.) and *Phacus longicauda* Ehrenb. rotate clockwise in the northern hemisphere. Inasmuch as the phototactic relation of the ciliates in general is negative, where a reaction exists, it seems probable that the inclusion of the minute symbiotic forms of algæ, *Chlorella vulgaris* Beyer, which gives the species its characteristic green apperance, has induced a change from a negatively phototactic to a positively phototactic condition, while the organism retained its original counterclockwise rotation. Small forms like *Chlorella* which contain chloroplasts, are generally positively phototactic so far as their responses to normal conditions are known.

Phacus longicauda (Ehrenb.) is an euglenoid about 100 μ in length, with comparatively flat wing-like expansions. The striæ covering the body are longitudinal. In swimming, however, many of the forms have the anterior part of the right expansion turned slightly down, while the left expansion is turned up in a similar manner. This gives their progressive movement a counterclockwise rotation.

In the southern hemisphere direct observation of the characteristic rotation has not been made, but inasmuch as the direction of the striæ indicates the direction of the rotation, certain evidence is available. Cunha (1913) in his studies of Protozoa from Brazil has figured several forms showing distinctly the arrangement of the striæ in the excellent plates drawn by himself. While it is not impossible that a careless investigator might focus on the lower part of the specimen, thus showing the reverse position of the striæ, the careful work of Cunha scarcely permits one to suggest such a criticism. It may furthermore be noted that the apparently counterclockwise rotating forms described by him are species quite different from the typical northern forms, while the forms which evidently rotate clockwise are closely allied to species from the northern hemisphere, and may have been introduced comparatively recently so far as evolutionary time is concerned.

The original development of the unicellular forms in the northern hemisphere with their subsequent introduction to the southern hemisphere by aquatic birds, etc., is well within the range of possibility and suggests that even should forms with reverse rotations be entirely absent from south of the equator, the hypothesis which has been proposed would by no means be invalidated.

Having presented the general facts as to the behavior of free-swimming microorganisms, it becomes advisable to consider the explanations which may exist as to the origin of the characteristic rotation. It seems impossible to attempt to account for such a character on the ground of "natural selection." One would be compelled to believe that the reverse rotation—the counterclockwise rotation of positive northern forms—possessed an elimination value, an almost indefensible proposition, particularly when forms like *Stentor polymorphus* and *Phacus longicauda* are considered as well as forms in the southern hemisphere which do not rotate in agreement with theory.

The most obvious explanation to be considered is that based on the influence which the sun in its apparent daily movement from east to west in the equatorial region may be supposed to have exerted on the flagellum (Fig. 2). This assumes that the flagellum is the orienting factor and that the sun has induced in it an east-west rotary-like or whip-like propelling movement. The consequent mechanical effect would be that in the northern hemisphere forms with a positive light reaction would rotate clockwise and those with a negative light reaction would rotate counterclockwise. Conditions would be reversed for those which might be present in the southern hemisphere during the evolutionary stage.

Conversely, negatively phototactic forms would develop a reversed or counterclockwise rotation by means of the influence of the light rays on the stroke of the light avoiding flagellum and their modified organs, the cilia. It is by no means necessary to believe that the stroke of

the flagellum should be one of rotation, although theory would imply a partial rotation in the primitive flagellate forms. The method of movement by means of the flagellum furnishes a problem of considerable difficulty which

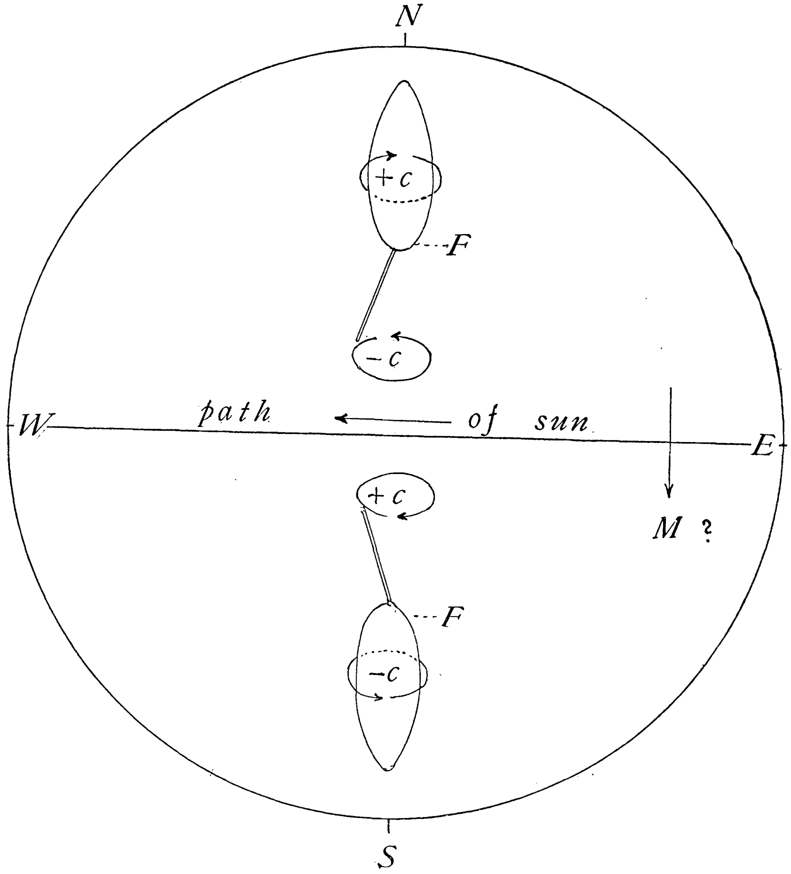


FIG. 2. Illustrating the theory as to the origin of axial rotation in aquatic microorganisms of the northern and southern hemisphere of the earth by the apparent movement of the sun from east to west. *N*, etc., north, etc.; *F*, flagellate organism; + *c*, — *c*, clockwise and counterclockwise rotation of organism (observer in front); + *c′*, — *c′*, induced clockwise and counterclockwise movement of flagellum; *M* ?, possible southern migration of forms which have retained primitive rotation.

has received attention from several investigators, notably Delage and Herouard (1896), Goodspeed and Moore (1911), Bütschli and others.

There are several inferences of an axiomatic nature

that follow from such an hypothesis. Forms near the neutral equatorial region may be assumed to possess a slower rotation than forms near the poles and at the same time there may be expected to occur a change in the relative angle which the striæ make with the longitudinal axis of the body, their direction becoming approximately parallel with that axis. The cosmopolitan distribution of unicellular organisms with the evident non-selective value of the character makes such a hypothesis difficult of demonstration. The application of statistical methods would be of interest, however.

A second explanation of the rotation direction, apparently, however, a negligible one, is on the basis of the angular velocity of the earth so far as it may have an influence on small bodies at its surface. With free-swimming microorganisms oriented in accordance with the axis of the earth during definite intervals and rotating in the same direction that the earth rotates, conditions are fulfilled for such a mechanical explanation. When, however, the relative dimensions of the earth and the organisms as well as the relative density of the earth, the water and the organism, are considered, it is difficult to believe that the explanation lies in this direction. While many of the forms are attached to some definite surface in the water during certain periods of their development, there are others which reproduce directly in the water and should this have been the primitive condition of development, the rotation of the earth would have been ineffective.

While the possibility of electrical forces may be mentioned as an influence, there are no facts known which allow an interpretation in this direction.

During the past two years a considerable number of experiments have been made in attempts to obtain some definite evidence as to the cause of the rotation. Obviously it would be of interest to maintain a culture of northern forms in the southern hemisphere or a culture of southern forms in the northern hemisphere. Efforts

to obtain living cultures from desirable localities, the Falkland Islands, New South Wales, the southern part of South America, etc., have thus far failed. A method, however, was devised by which it seemed theoretically possible to subject northern flagellates to an environment similar to that of the southern hemisphere. A clinostat (Fig. 3) having a clockwise rotation of fifteen minutes

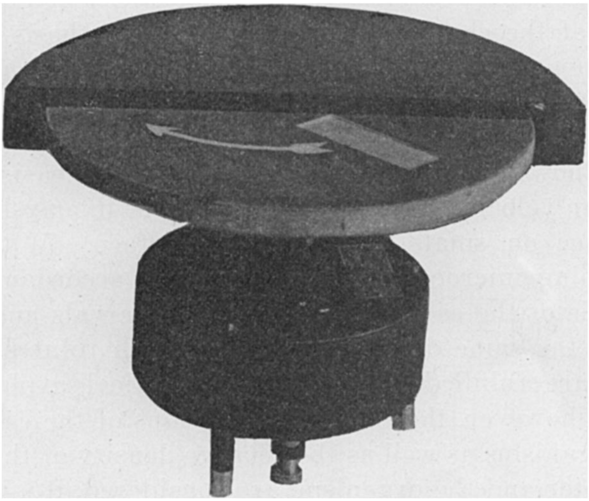


FIG. 3. A clinostat arranged for the purpose of subjecting northern flagellates, etc., to an apparent west-east movement of the sun, the covered portion being toward the north.

was procured, a circular table ten inches in diameter fitted to this, and the northern half covered so that the revolving table containing slides in excavated recesses would pass into darkness on one side and emerge moving from east to west. Thus the apparent path of the sun so far as the organisms were concerned would be from west to east. The larger unstriated *Euglena* have been used almost entirely in the experiments, inasmuch as it would apparently be impossible to change the direction of rotation in forms like *Euglena spirogyra* Ehrenb., *Phacus pyrum* (Ehrenb.), etc., where the striæ are carinate in structure with an angle almost if not entirely precluding a rotation in the direction opposite to that in which they were accustomed to turn.

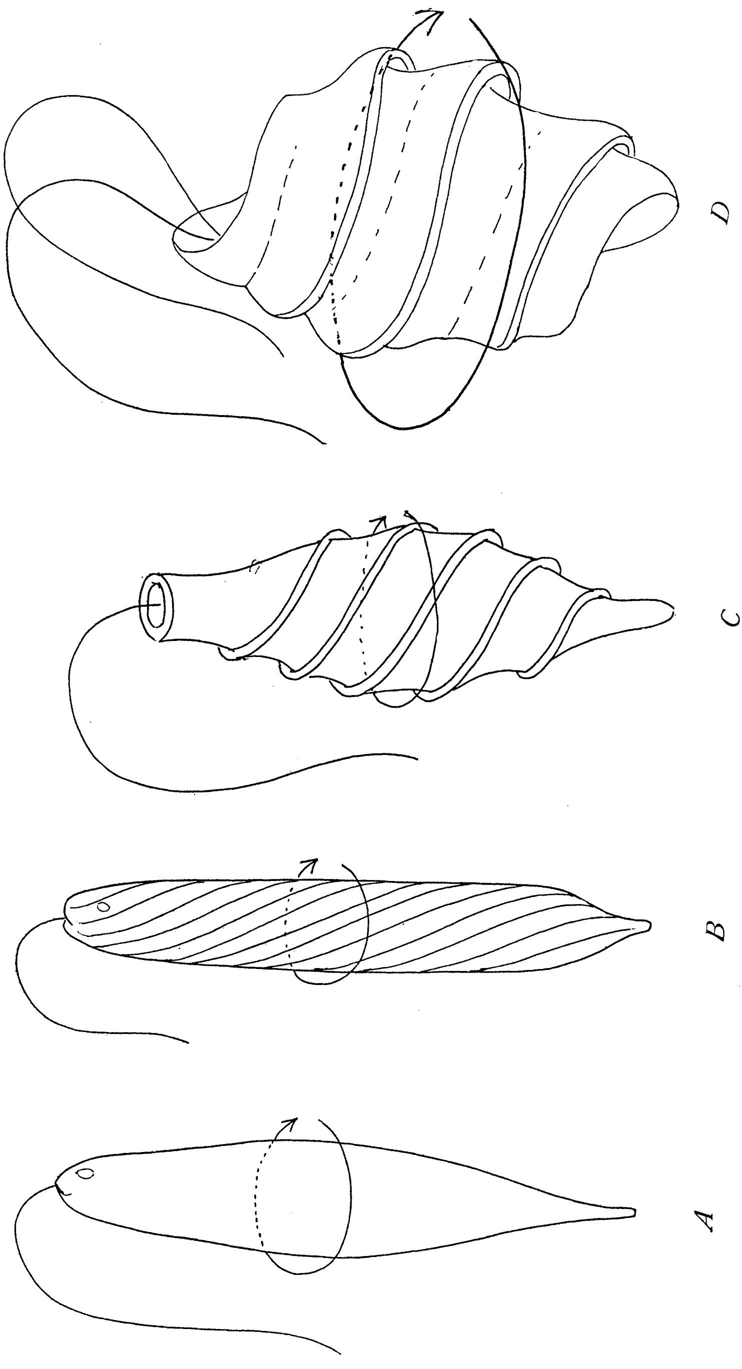


FIG. 4. Flagellate forms from the northern hemisphere illustrating the development of the left-hand striæ. A, *Euglena hæmogranulata* Walton (Ohio); B, *Euglena spirogyra* Ehrb. (Ohio); C, *Urceolus costatus* Lemm. (Europe); D, *Heteronema spirale* Klebs (Europe).

While there has been a large amount of data obtained, thus far no evidence shows that either a "reversal" or a "slowing up" of the rotation may be produced in any of the individuals utilized.

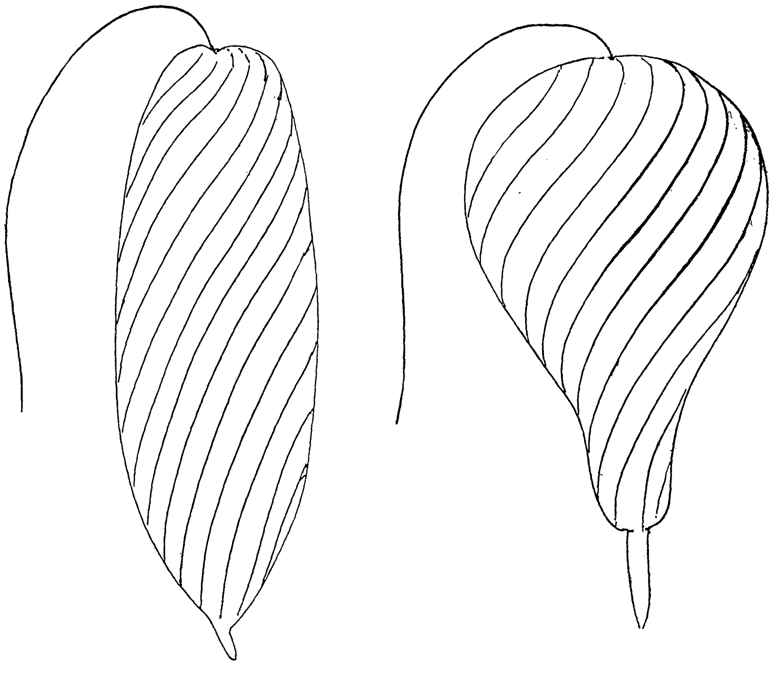
Even though it may not be possible to change the direction or the period of rotation in "adult" forms, may not such changes be produced in encysted forms or during a period when gametes are developed. Experiments are yet to be made with individuals in an encysted condition, and with material available it will be possible to utilize gamete-producing forms. That *Euglena* has a sexual cycle was pointed out by the writer nearly ten years ago (Walton, 1909).[7] Certain forms encyst, the cysts subdividing to approximately a 16-cell stage, small flagellate gametes emerge and conjugate. An experiment of this nature involves a discussion of the environmental effect on germ cells as compared with somatic cells, but does not affect the issues with which we are concerned in the present paper.

There are many other questions of interest which arise in a study such as outlined. For instance, what has been the origin of the striæ which are much specialized in many forms, although entirely absent in other forms (Fig. 4) so far as visibility with the microscope is concerned. The majority of the positive northern forms have "left-handed" striæ, a smaller number have longitudinal striæ, while a considerable number appear to have no striæ. None have been found with "right-handed" striæ. At first one may be inclined to attribute such a character to natural selection, but when one commences to ascertain the value of the character on the basis of progression, rotation and axial angle, such a conclusion seems less certain. There are a few facts that appear evident. First that the development of the striæ has been at a considerably later period than that of the rotation direction. Second that the relative position of the striæ has been largely dependent on the rotation. Third,

[7] Paper presented at annual meeting of Ohio Academy of Science, 1908.

that the development of the striæ has in many forms proceeded so far that a reversal rotation seems an impossibility.

The presence of a considerable number of other groups which have "left-handed" spirals so far as observation goes, is of interest. The various genera of Spirochætes, as well as *Spirulina* and *Arthrospira* among the *Cyano-*



A *B*

FIG. 5. Flagellate forms from the southern hemisphere, Rio de Janeiro, Brazil (from Cunha), illustrating the development of the right-hand striæ. *A, Phacus bacilifer* Cunha; *B, Leptocinclis piriformis* Cunha.

phycoidea (*Cyanophyceæ*) may be mentioned. The twining of plants may, in the final analysis, be attributable to the same cause.

Other related problems are the pendulation theory of Simroth (1912) relative to bipolar distribution, and the tropism theory as outlined by Verworn (1894), in connection with the excitation contraction of the flagellum.

V

Having indicated some of the difficulties existing along the lines of established research in the efforts to account for the derivation of the fundamental heritable units making up an organism and having presented a series of observations suggesting that a new perspective may be obtained by utilizing methods of attacking the problem somewhat different from those hitherto employed, the particular purpose of the paper is accomplished.

It may be asserted by some that such an attempt at a summary disposal of the existing evidence as to the actual origin of characters represents an unfortunate type of destructive criticism. Furthermore, that the acceptance of the validity of the arguments as to the long predetermined nature of the genes or subgenes, leads us once more in the direction of the somewhat antiquated theory of preformation. It is not impossible that these views are in part justified. Nevertheless it is well within the bounds of propriety to occasionally inquire as to whether the enthusiasm developed for a special discovery has not resulted in too broad an application of its principles. The mutation theory particularly as developed by Morgan is of interest. It is circumscribed at least in part by the phenomena of mendelian inheritance, and it is evident that one should look farther for the facts which may assist in explaining the real origin of the diversity of living things.

If additional studies support the view suggested by the facts here presented, namely, that characters of a physiological nature may be produced by environmental causes, and that these in turn may demand the correlation of morphological characters regardless of the origin of the latter, an important step will have been made in accounting for the primary differentiation of organisms. The later secondary differentiation through the combinations of units which have thus arisen, and which attains its maximum in the complex multicellular animals and plants, offers no particular difficulties in its explanation.

Furthermore, such an idea is more in harmony with the paleontological evidence as presented by Osborn (1912) and others, than one based on the mutational idea, and it is to fossil forms that one must look for the all-important historical record.

Should one propose a hypothesis of an ultimate unit, slightly plastic as to its immediate environment, but subject to the permutations and combinations of a mendelian type, and possessing a definite qualitative condition determined by prolonged environmental action, the picture is not at all so fanciful as some might at first thought insist.

The practical importance of such a viewpoint in its application to the problems of animal and plant breeding lies in the realization that new forms can not be created, but merely new combinations uncovered during the comparatively brief epochs of time which human intelligence has for working out the processes. Thus one returns to genetics.

In summarizing the paper, the following conclusions are suggested:

I. The heritable characters in general which make up an organism arise from preformed units in the nature of genes or subgenes that have been in existence during long geological periods of time. There are at present no criteria available in modern genetics by which an apparently new gene may be distinguished from one long in existence; furthermore, there is doubt as to whether new genes are actually arising in multicellular organisms. The change of a gene in a given direction, whether it be considered as a morphological unit or a chemical condition followed by the return to its original condition, suggests its composition of combinational sub-units, and is an argument against the idea that anything actually new has come into being during its series of so-called mutations. Such a conclusion receives additional support from the presence of apparently identical genes which exist in distinct species of organisms separated during

long epochs of time, as well as from the evidence of the non-contamination of genes during diverse environments.

II. The mutations demonstrated by DeVries and others, together with the variations obtained by Castle, are to be interpreted as a result of the combinations of existing genes. The mutations noted by Morgan and his associates, as evidenced from recurrence and stability, are in the nature of modal fluctuations having no definite cumulative value.

III. The direction of axial rotation in aquatic microorganisms is best explainable on the basis of the apparent east-west motion of the sun having influenced the movement of the organs of locomotion. Thus the character becomes one acquired from external stimuli, and the persistence of reverse forms in both the northern and southern hemispheres indicates the hereditary nature of the character. Morphological characters, such as the striæ, etc., may arise in a similar manner or through selection. By correlation with the preceding characters, a cumulative and irreversible effect is produced.

IV. The primary factors in evolution are environmental and thus dynamic. The secondary factors of a combinational nature are gradually approaching a limiting maximum value, and are thus becoming static.

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